DISTURBANCE TO CORAL REEFS IN ACEH, NORTHERN SUMATRA: IMPACTS OF THE SUMATRA-ANDAMAN TSUNAMI AND PRE-TSUNAMI DEGRADATION

BY

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ABSTRACT

The Sumatra-Andaman tsunami of 26 December 2004 was the first to occur in areas for which good ecological data existed prior to the event and consequently provided a unique opportunity to assess the effects of this type of natural disturbance in tropical marine ecosystems. Less than 100 days after the event we visited 49 sites on coral reefs in northern Aceh, Indonesia, all within 300 km of the epicentre, to determine the nature and extent of tsunami damage and pre-tsunami disturbance. Reef fish diversity and abundance were also assessed in relation to tsunami impact and existing marine resource management regulations. At these sites, the initial damage to corals, while occasionally spectacular, was surprisingly limited and trivial when compared to pre-existing damage most probably caused by destructive fishing practices. The abundance of up-turned corals was highly dependent on habitat and largely restricted to corals growing in unconsolidated substrata at depth, a feature we believe unique to tsunami disturbance. Other evidence of tsunami damage, including the abundance of broken corals and recently killed corals was patchy and varied unpredictably between sites: reef aspect, geographic location and management regime had no significant effect on these variables with the exception of broken live corals which were more abundant at locations where the tsunami was larger. Interestingly, there was little correlation between damage variables, suggesting the type of damage observed was strongly influenced by which corals were present at a particular site or depth. In contrast, reef condition was clearly correlated with the management regime. Coral cover was on average 2-3 times higher on reefs managed under the traditional Acehnese system, Panglima Laut, and in the Pulau Rubiah Marine Park when compared to open access areas. Turf algae and coral rubble were 2-3 times

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more abundant in open access sites compared with managed areas. These results are consistent with a history of destructive fishing practices, such as bombing and cyanide fishing in open access areas. Coral reef fish abundance and diversity did not differ among management zones, despite the fact that Pulau Rubiah Marine Park has been closed to fishing for 10 years. However, there were consistent differences in the structure of the reef fish assemblages among these zones. For example, the near absence of chaetodontids at open access sites is probably the result of low coral cover. The high abundance of scarids and acanthurids in the Marine Park, suggests that while management efforts have failed to allow fish to increase in abundance, they have been effective at protecting certain species. The tsunami had no detectable affect on reef fish assemblages at these sites. This lack of major damage means that neither the conservation priorities nor the risks to reefs have been changed by the tsunami and it is vitally important that resources are not directed to short term, small scale, rehabilitation programs which will not reverse

INTRODUCTION

long term declines in reef condition which were evident at many of our sites.

Disturbance has a significant role in determining the structure and dynamics of ecological communities (Pickett and White, 1985; Petraitis et al., 1989), especially in coastal marine habitats, which appear particularly susceptible to a wide range of natural and anthropogenic disturbances (e.g., Alongi, 2002; Hughes et al., 2003). These disturbances, including severe tropical storms, temperature fluctuations, terrestrial run-off, and diseases, vary in their scale, intensity and frequency (Hughes and Connell 1999), contributing to extreme spatial and temporal variability in the biological structure of shallow-water marine communities (Karlson and Hurd, 1993). There is increasing evidence, however, that effects of natural disturbances are being further compounded by anthropogenic stresses leading to directional changes in the structure of marine habitats. In the extreme, synergistic effects of multiple chronic disturbances lead to irreversible and fundamental shifts in biological structure. On coral reefs, chronic over-fishing combined with excess nutrients has led to permanent shifts from coral-dominated to algal-dominated benthos (Done, 1992; Hughes, 1994; McCook, 1999). This in turn may have significant repercussions for the long-term survival of coral associated reef fishes (reviewed by Wilson et al., 2006).

Coastal marine habitats in Indonesia have been subject to a long-history of disturbance from destructive fishing practices (Edinger et al., 1998) combined with severe episodes of sedimentation and increased turbidity associated with monsoonal rains and land based runoff (McManus, 1988; Hopley and Suharsono, 2002). On December 26th, 2004, these habitats were further subject to an extreme punctuated disturbance in the form of the Sumatra-Andaman earthquake and subsequent tsunami. The spatial scale and magnitude of this tsunami has no historical precedent and many aspects of the event, such as the length of the fault line and the speed of the slip suggested it was almost unique (Lay et al., 2005, Vigny et al. 2005). Estimates of the return time for tsunamis greater than 10 m wave height are 1000 years for the Indian Ocean (Tsunami Risks Project,

2005) indicating that this was indeed a rare natural disturbance. While smaller tsunamis are relatively common, for example since 1883, 35 tsunamis have occurred in Indonesia alone (Birowo et al., 1983), there are as yet few quantitative studies of the damage they cause to coral reef communities (Tomascik, 1997a, 572-4) and consequently the event provided a unique opportunity to assess the effects of this type of natural disturbance in tropical marine ecosystems.

Initial reports of damage to coral reefs following the tsunami suggested that greatest impacts were in Indonesia and the Andaman Islands (UNEP, 2005). In Indonesia, initial assessments based on satellite imagery suggested that 97,250 ha of coral reef habitat was affected with a potential loss of 3061 ha valued at \$332 million dollars (Anon, 2005). Region reports have since revealed that tsunami damage varied widely, and often unpredictably. For example, Baird et al. (2005) described the damage as occasionally spectacular, but surprisingly limited, given the proximity of their sites in Aceh to the epicentre of the December 26, 2004 earthquake. Damage to the reefs of Thailand (Comley et al., 2005; Phongsuwan and Brown, 2007) and the Maldives (Gunn et al., 2005) was similarly patchy, but generally low. In contrast, widespread damage was reported to reef habitats in the Andaman and Nicobar islands (Kulkarni, 2001), Sri Lanka (CORDIO, 2005a; Meynell and Rust, 2005) and even the Seychelles (Obura and Abdulla, 2005), which is perhaps surprising given the distance from the epicenter of the earthquake. The only study to present data from both before and after the tsunami detected no change to shallow coral assemblages on Pulau Weh in Aceh (Baird et al., 2005), despite an estimated run-up height of 5 m at this location (USGS, 2005).

In this study we assessed the condition of coral reefs in northern Aceh region of Sumatra to determine the effect of the Sumatra-Andaman earthquake and tsunami on coral reef communities. The status of coral reef communities (both coral and fish communities) was examined against a background of considerable prior disturbance. Most importantly, reefs in northern Aceh have been subject to destructive fishing practices, such as cyanide fishing and bombing, which have devastating effects on fish stocks as well as the benthic reef habitats. Accordingly, we sampled sites under 3 different management regimes; open access areas, Pulau Rubiah Marine Reserve, and the tradition Acehnese management practice, Panglima Laut.

METHODS

In April 2005 (<100 days after the tsunami) we visited 49 sites in northern Aceh located within 300 km of the epicentre of the earthquake (Fig. 1). Study sites were located within three different management regimes; 1) a central government managed marine tourism reserve centered around Pulau Rubiah, which we will call Kawasan Wisata, 2) community based traditional Acehnese marine management system known as Panglima Laut, and 3) open access areas. To document current reef condition and assess potential tsunami damage we used the rapid assessment techniques recommended by the World Conservation Monitoring Centre (CORDIO, 2005b). Reef fish abundance and diversity were also assessed a subset of these sites.

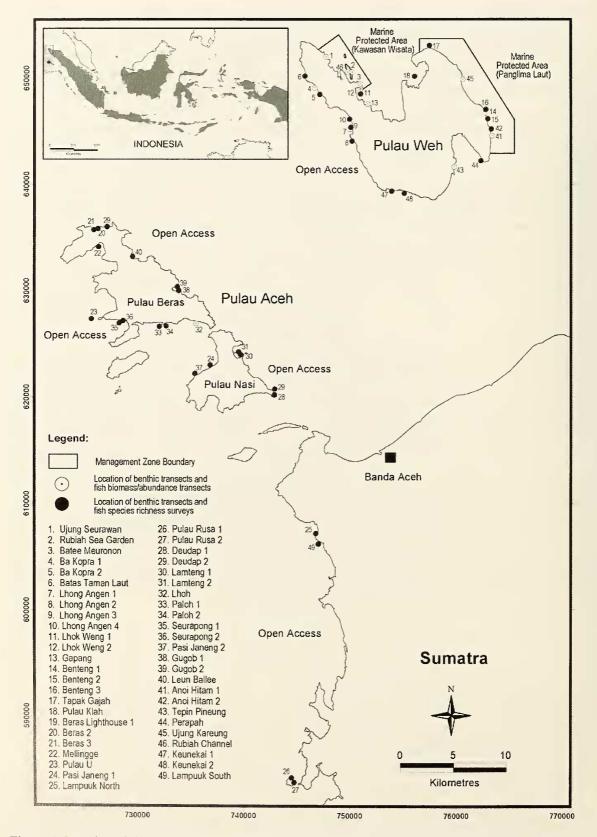


Figure 1. Location of sites for assessment of coral reef substrate variables (47 sites) and coral reef fish (31 sites), northern Aceh, Indonesia.

Surveys were conducted at 47 of the 49 sites to assess the biological and physical structure of the reef benthos, and also to quantify recent physical damage attributable to the tsunami (Fig. 1). At each site 16-32 replicate 10 x 1 m belt transects were conducted on the reef crest (0-2 m) and/or the reef slope (3-10 m). On these transects the percentage cover of the following variables was recorded, three describing reef condition: 1) live coral cover, 2) coral rubble, and 3) turf algae; and three indicative of recent reef damage: 1) coral colonies that were up-turned or displaced (Fig. 2E), 2) attached colonies with partial mortality or broken branches (Fig. 2F), 3) recently killed colonies (Fig. 2B). The following categories were recorded as estimates of cover following CORDIO (2005b): 0% = 0; 1-10% = 5; 11-30% = 20; 21-50% = 30; 51-75% = 62.5; 76-100% = 87.5). For statistical analysis, the mid-point of each category was used to calculate mean values for each group.

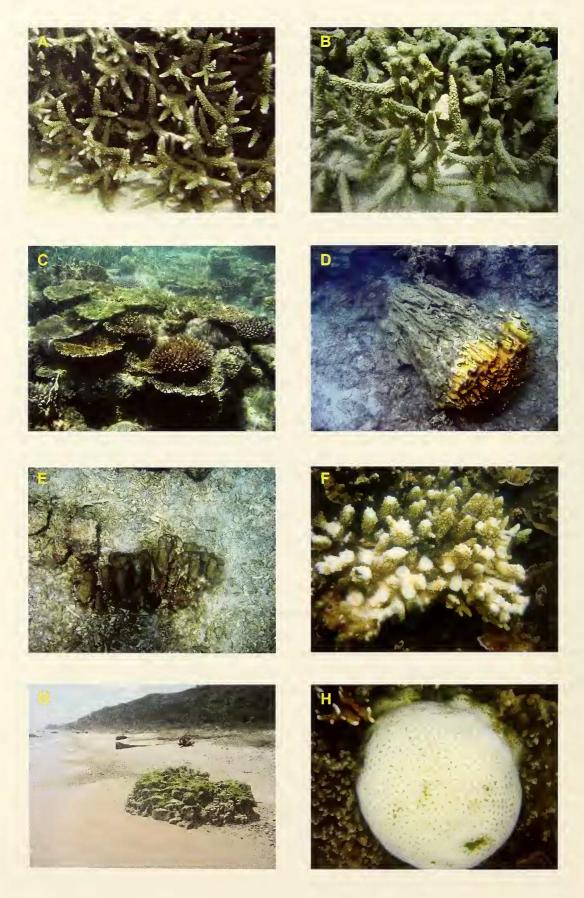
To assess potential impacts of the tsunami on reef associated fauna, species diversity of reef fish assemblages was quantified during 20 min timed swims at 31 sites. Two divers (SP, TK) swam along a pre-designated path recording all species observed and the lists combined to provide an estimate of species richness for each site. Surveys were conducted along a zig-zag path starting at ~25 m depth and extending to the reef crest. The total area surveyed was approximately 300 m x 100 m per site.

The abundance of fishes within each of 45 major reef fish families was documented at 13 sites: 3 located within Kawasan Wisata where all fishing is prohibited; 3 within Panglima Laut where only artisanal line fishing is permitted; the remaining 7 sites were located in open use areas, where fishing activities are largely unregulated, and includes line-fishing, muro-ami (a particularly destructive form of netting), netting, trapping, and spear fishing. The size and number of all fishes within each of 45 families were recorded simultaneously using 3 replicate 50 m transects on the reef crest (<2 m). Transects were run parallel to the reef crest and spaced >5 m apart. The transect line was delineated using a 50 m fibreglass tape, along which small fishes (<10 cm TL) were surveyed in a 2m wide path and larger fishes (>10 cm TL) were surveyed in a 5 m wide path.

The different regimes under which sites were managed should influence reef condition. Consequently, we tested for significant difference in mean cover of coral, filamentous algae and coral rubble among management zones using a 2-way ANOVA. Factors in the model were management (fixed; 3 levels, as described above) and site nested with management (random; 4 to 28 sites per management regime). For these variables the analysis was repeated twice; once for shallow sites (n = 38), and again for deep sites (n = 45) because at many sites transects were only run at one depth.

Tsunami run-up, which was evident throughout the region as a prominent scar from which vegetation had been stripped, was higher in Pulau Aceh and the mainland when compared to Pulau Weh. Measurements by the United States Geological Survey (USGS) confirmed these observations, recording maximum run-up heights in Pulau Aceh and the mainland as 22 m and 26 m respectively, 4 to 5 times higher than on Pulau Weh (~5m) (USGS, 2005). In addition, our initial observations (see Baird et al., 2005) suggested that damage was habitat specific, in particular, up-turned corals appeared to be more abundant at depth (> 2 m) than in the shallows (< 2 m). Consequently, we used a 3 way-ANOVA to test for mean differences in the proportion of the 3 damage variables (upturned coral, broken coral, recently killed coral) among locations, sites and between





depths. Factors in the model were location (fixed; 2 levels, Pulau Aceh/mainland, Pulau Weh), site nested within location (random; 17 and 24 levels) and depth (fixed: 2 levels, shallow and deep) which was crossed with both location and site nested within location. Only up-turned coral differed significantly between depths, so to increase the quantity of data for the other variables we ran a 2-way ANOVA as described above for the reef condition variable using transects from each depth.

Much work on tsunami damage to coastlines indicates that the angle of incidence between the tsunami and the coastline can influence the degree of damage, and shorelines fronting the tsunami would be expected to suffer greater damage than shorelines in the lee of the tsunami. Consequently, we used a 2-way ANOVA to test for differences in the mean proportion of up-turned coral, broken and recently killed coral among sites facing north, south, east and west. Factors in the model were reef aspect (fixed; 4 levels, north, south, east, and west facing reefs), and site nested within reef aspect (random; 3 to 19 site per aspect). Once again, to increase the data available for analysis shallow and deep transects were analysed separately. All damage and reef condition variables were arcsine transformed and the normality and homoscedasticity of the transformed data examined with graphical analyses of the residuals. Analyses were completed using SYSTAT v10.2.

Corals reef fish may also be influenced by different fishing restrictions enforced within management zones. Consequently, we tested for significant difference in mean abundance of coral reef fish among management zones using a 2-way ANOVA. Factors in the model were management (fixed; 3 levels, as described above) and site nested with management (random; 3 to 6 sites per management zone). Only a single estimate of diversity was made at each of 31 sites. Consequently, 1-way ANOVA was used to test for differences in mean species richness among management zones (fixed; 3 levels) with site values providing the replication within management. Both variables were $\log_e (x+1)$ transformed to improve homogeneity and normality, and analyses were completed using SYSTAT v10.2.

To explore spatial variation in the composition of reef fish assemblages, MANOVA was used to test for variation in the relative abundance of five major families (Acanthuridae, Chaetodontidae, Labridae, Scaridae, Serranidae and Pomacentridae) among 13 sites for which these data were available. All data were log_e transformed prior to analyses to improve homogeneity and normality, and analyses were completed using SPSS v11.0.

Figure 2. A. Healthy colony of *Acropora muricata* in 1 m at site 49, November 2000. B. The same colony as in Fig 2A in April 2005. Despite an estimated wave height of over 12 m, the colony is still intact, however, the tissue has been smothered by sediment stirred up by the tsunami. C. Healthy reef in the shallows of Pulau Rubiah Marine Park site 46 in April 2005. D. A collapsed colony of *Heliopora* sp. Site 11
E. A buried *Porites* colony in approximately 3 m depth. Interestingly, this colony was less than 20m from the healthy reef in Fig. 2C, demonstrating the different impact of the tsunami on corals firmly attached to reef or rock when compared to corals growing in sand or rubble. F. Broken branches in an *Acropora* sp. site 26 in 0.5 m depth. The wounds have healed, however, the polyps have yet to begin growing again, suggesting the injury is recent, and most probably cause by debris mobilized by the tsunami. G. A large *Porites* colony at site 27. The turbidity at some sites, in particular on the mainland and in Pulau Aceh, was very high, and continues to pose a threat to coral assemblages.

RESULTS

At these sites on the north and west coast of Aceh, where the tsunami was most ferocious, the initial damage to coral reefs, while occasionally spectacular (Fig. 2G), was surprisingly limited. Furthermore, damage was very patchy with often pronounced difference between adjacent sites. Tsunami damage was largely unpredictable: neither reef aspect, geographic location (a proxy for tsunami intensity) nor management zone had a significant effect on the amount of damage. The only clear patterns were a higher proportion of up-turned corals at depth and a higher proportion of broken corals on reef crests at Pulau Aceh and mainland sites. Reef condition, however, varied widely within the region and was clearly correlated with management regimes. Coral cover was high, and the cover of algae and rubble low at Kawasan Wisata and Panglima Laut sites. In contrast, coral cover was low and the cover of algae and rubble was high at open access sites.

The mean proportion of overturned corals was significantly higher at depth (shallow sites: 3.3 ± 0.35 ; deep sites; 7.6 ± 0.43 ; $F_{1, 33} = 9.4$, P = 0.004). This pattern was evident at most sites, except where the damage was low, such as most Panglima Laut sites (Fig. 3A), and at these sites, not surprisingly, there was no difference in the mean proportion of up-turned coral between depths, causing an interaction between depth and site (management) (F_{33, 1464} = 4.1, P < 0.001). While there was considerable variation among sites (management), the mean proportion of overturned corals did not differ among management zones (F_{2, 33} = 0.500, P = 0.611). All management regimes had some sites with moderate abundance of overturned coral and some sites with no overturned corals (Fig. 3A). Neither reef orientation, nor geographic location had any significant effect on the abundance of up-turned corals on either the reef crest or reef slope.

The mean proportion of broken live coral was significantly higher in the shallows at Pulau Aceh and mainland areas (21.6 ±1.65SE) compared with Pulau Weh (5.7 ±0.72SE) ($F_{1,34} = 6.565$, P = 0.0145) (Fig. 3B) but this pattern was not repeated at depth ($F_{3,41} = 2.3$, P = 0.09). The abundance of broken live coral was not significantly affected by management, depth, orientation, or geographic location on either the reef slope, or the reef crest. The abundance of recently killed corals was similarly unpredictable, with a few sites within each location experiencing high mortality, but at most sites no recently killed corals where recorded (Fig. 3C).

Damage variables were poorly correlated. Transects with a high proportion upturned corals did not, generally, have a high proportion of broken coral ($r^2 = 0.087$), or recently killed coral ($r^2 = 0.003$). While there was weak correlation between broken coral and recently killed coral, only 15 % of the variation was explained by the relationship.

All measures of reef condition (i.e. live coral cover, turf algae, coral rubble) varied among management zones. Coral cover was significantly higher in the shallows at Kawasan Wisata (31.7±2.8) and Panglima Laut (52.2 ± 2.2 SE) sites when compared with open access sites (19.3±0.9) ($F_{2,35}$, = 8.4, P < 0.001) (Fig. 4A). This pattern was even more pronounced at depth where coral cover at Panglima Laut (44.8 ± 2.7 SE) and Kawasan Wisata (25.8±1.5SE) sites was 3 to 10 times higher than at open access zones (3.8±0.5) ($F_{2,42}$ = 5.4, P < 0.008). In contrast, to this pattern both turf algae ($F_{2,35}$, = 8.4, P < 0.019; Fig. 4B) and rubble ($F_{2,35}$, = 3.7, P < 0.035; Fig. 4C) were 10 – 20 times higher

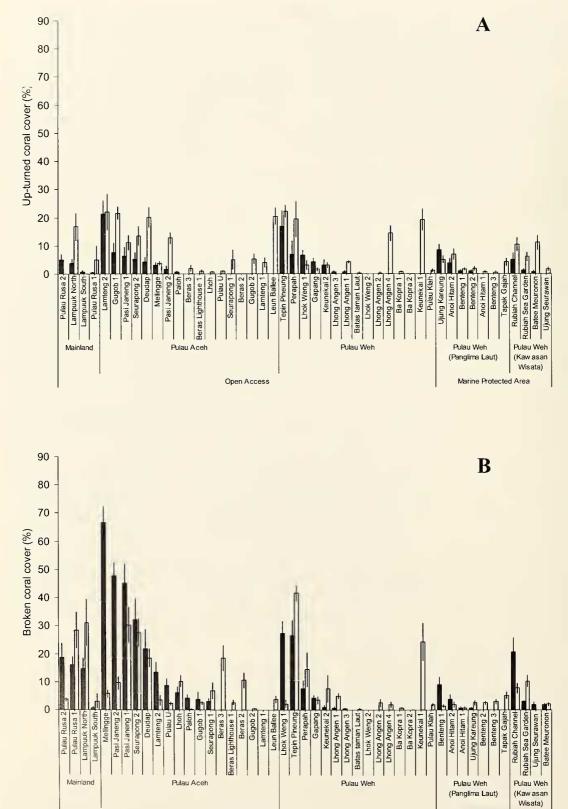
at open access sites (algae = 33.9 ± 1.4 SE; rubble = 20.4 ± 1.2 SE) when compared to Panglima Laut (algae = 17.7 ± 2.4 SE; rubble = 1.5 ± 0.5 SE) and Kawasan Wisata sites (algae = 3 ± 0.9 SE; rubble = 0.4 ± 0.2 SE).

While the direct effects of the tsunami on the function of coral reef ecosystems were relatively minor, changes in the sediment regime following the tsunami have caused localized mortality and continue to threaten some reefs. For example, a previously flourishing *Acropora* assemblage at the southern edge of the fringing reef at Lampuuk (site 49, Fig. 1) was smothered by sediments causing complete mortality (Fig. 2B) compared with previous surveys in March 2003 (Fig. 2A). While these dead colonies were still intact in April 2005, by December 2005 they had completely disappeared. Other examples of indirect effects from the tsunami include bleached *Acropora* and faviid colonies (Fig. 2H) at sites 25, 27 and 28.

A total of 358 species of reef fishes were recorded across all 28 study sites surveyed during this study. The most speciose families were the Pomacentridae (59 species), Labridae (47 species), Chaetodontidae (32 species), Acanthuridae (28 species) and Scaridae (24 species). Species richness of reef fishes varied greatly among sample sites, ranging from 14 species at Pulau Rusa 2 (site 27, Fig. 1) to 103 species at Gugob 1 (site 38) on the north-east side of Palau Beras (Fig. 5). The species richness of coral reef fishes varied greatly even among closely positioned sites. For example, 73 species of reef fishes were recorded at Paloh (site 33) on the southern side of Palau Beras, whereas only 19 species were recorded at Lhoh (site 32), located <5 km away. Mean species richness did not vary among management zones and ranged from $36.00 \pm 3.46SE$ at Panglima Laut sites to $48.7 \pm 5.47SE$ at open access sites ($F_{2,28} = 0.45$, P = 0.645).

The mean abundance of reef fishes (averaged across all families) varied by an order of magnitude among sites, ranging from 4900 (± 167.73SE) fishes per hectare at Anoi Hitam 1 (site 41), up to 94,968 (± 68,695SE) fishes per hectare at Rubiah Channel (site 46) (Fig. 6). The overall abundance of fishes varied greatly among sites (df_{2,10}, F = 4.32, P < 0.05), but there was no significant variation attributable to differences in management (df_{2,10}, F = 0.36, P > 0.05). The most abundant family of fishes was the Pomacentridae, which accounted for more than 55.9% of all fishes counted. The next most abundant families of fishes were the Acanthuridae, Serranidae and Chaetodontidae, although families comprising mostly small or cryptic fishes (e.g., Apogonidae or Blennidae), which comprise a significant component of the ichthyofauna on coral reefs (Munday and Jones 1998) were not surveyed.

While there was little difference in either the abundance or diversity of fishes among management zones, the structure of coral reef fish assemblages did vary significantly among both management zones (MANOVA, Pillia's Trace = 1.04, $F_{14,42}$ = 3.25, *P* = 0.002) and sites within each management zone (MANOVA, Pillia's Trace = 3.10, $F_{70,182}$ = 2.06, *P* < 0.001). The structure of coral reef fish assemblages at sites within the Kawasan Wisata was fairly distinctive, characterized by high abundance of Acanthuridae (Fig. 7). Similarly, the three sites from the Panglima Laut all had very similar fish assemblages, with much higher abundance of Labridae compared to the Kawasan Wisata (Fig. 7). Notably, fishes from the families Acanthuridae, Labridae Chaetodontidae, and Serranidae all tended to be more abundant at Kawasan Wisata and Panglima Laut sites compared to open access areas (Fig. 7). Variation among sites within



Open Access

Marine Protected Area

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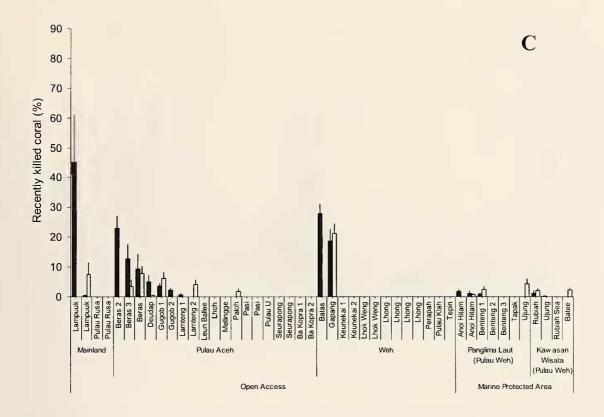
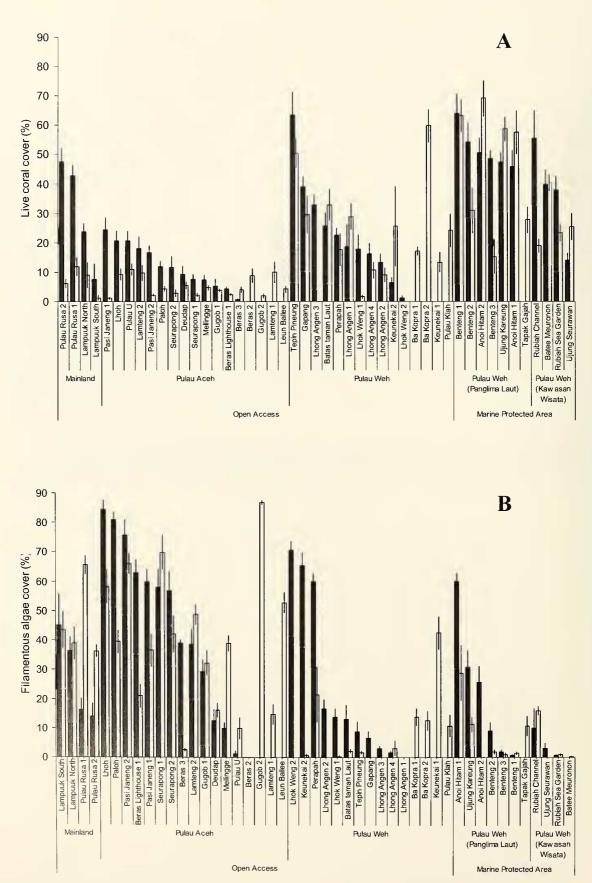


Figure 3. Spatial and habitat variation in damage variables at 47 sites in northern Aceh. Values are the mean + one standard error. Black bars represent transects run in the shallows (≤ 2 m) and white bars represent transects run at depth (≥ 2 m). A. Up-turned coral. B. Broken live coral. C Recently killed coral.



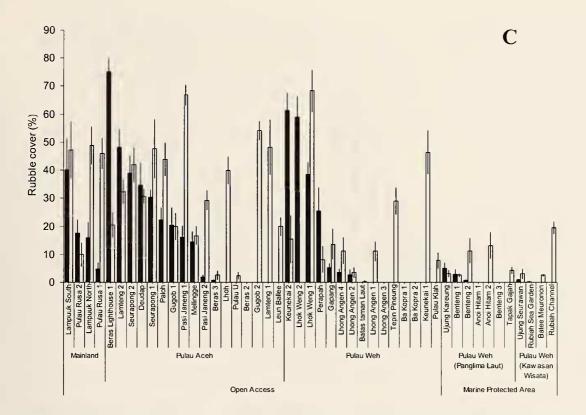


Figure 4. Spatial and habitat variation in reef condition variables at 47 sites in northern Acch. Values are the mean + one standard error. Black bars represent transects run in the shallows (<2 m) and white bars represent transects run at depth (>2 m). A. Live coral. B. Filamentous algae. C. Rubble.

each management regime was highest among open access sites, which did not appear to be grouped by geographic proximity. For example, Lhok Weng 1 (site 11) and Gapang (site 13), which are open access sites located within 1 km of each other on the northern side of Pulau Weh, had very different fish assemblages (Fig. 7). The fish assemblage at Gapang, and also Batee Meuronon (site 3), were most similar to those of sites within the Panglima Laut, with high abundance of Labridae, Chaetodontidae and Serranidae, whereas these families of fishes were rare at most open access areas, especially Lhok Weng 1 (site 11) and Tepin Pineung (site 43) (Fig. 7).

DISCUSSION

Our detailed, large scale and quantitative survey of the reefs in northern Aceh clearly demonstrates that the first reports of tsunami damage from this region were grossly exaggerated. The value of such qualitative assessments must be questioned, they are all too easy to make, and because they are typically the first available news, they capture undue attention. Furthermore, the uncritical repetition of these studies (e.g., Tun et al. 2005) must also be questioned, because it only serves to perpetuated the myth, and obscure its provenance. The overwhelming picture from the majority of reports from the Indian Ocean (Baird et al., 2005; Brown, 2005; Phongsuwan and Brown, 2007; Comley et al., 2005; Gunn et al., 2005) is that the damage caused to coral reefs by the Dec 26 earthquake and tsunami was rarely of ecological significance, and at our sites in northern Aceh, tsunami damage was trivial when compared with that caused from chronic human misuse.

Few clear patterns were evident in the tsunami damage observed: neither reef aspect, geographic location (i.e. tsunami intensity) nor management zone (i.e. reef quality) significantly affected any of the damage variables, with the one exception being high abundance of broken live coral on mainland and Pulau Weh reef crests. This is perhaps surprising, and contrasts with results reported elsewhere (Baird et al., 2005; Brown, 2005; Chatenoux and Peduzzi, 2005). However, tsunamis interact with submarine and coastal topography in complex ways and interference, resonance, and reflection can concentrate the force of the tsunami in unexpected locations, such as the lee of islands, small embayments and channels (Tsunami Risks Project, 2005). The earthquake of 26 December 2004 generated a tsunami in Aceh which consisted of at least 3 main waves (a wave train), preceded by an initial draw down (Lay et al., 2005). The first wave was estimated at 12 m by eyewitnesses before it broke on the reefs on the Acehnese coast. The second wave was considerably larger, with flow heights at the coast ranging from 10.0 to 15.0 m (Borrero 2005). Indeed, the northern tip of Aceh and the islands to the north were in effect hit by two wave trains, one from the north and one from the west (Borrero 2005). With such a complex tsunami event up such a large scale in an area with many islands of contrasting geography untangling the features that made one reef more susceptible to damage than another is possibly intractable.

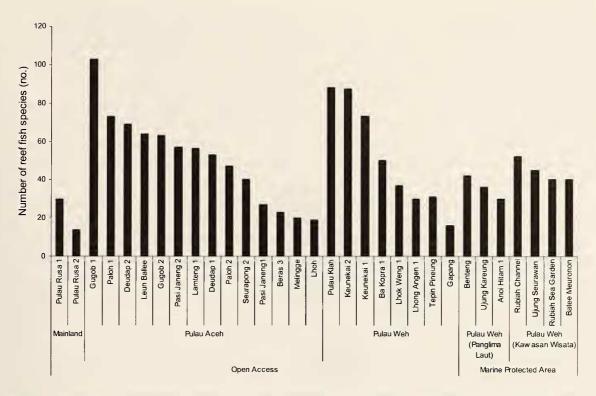


Figure 5. Reef fish species richness in within 3 geographic regions (Mainland, Pulau Acch, Pulau Weh) and 3 management zones (Open Access, Kawasan Wisata, Panglima Laut) in northern Aceh, Indonesia.

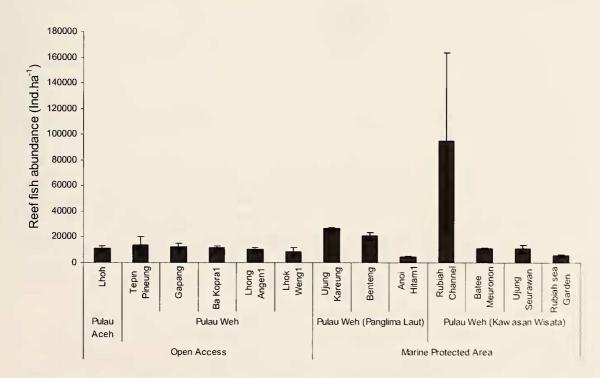


Figure 6. Reef fish abundance (ind.ha-1) (mean \pm SE) within 2 geographic regions and 3 management zones (Open Access, Kawasan Wisata, Panglima Laut) in northern Acch, Indonesia.

The one clear pattern was a higher abundance of overturned colonies growing in unconsolidated substratum below 2 m. Corals firmly attached to solid substratum were largely unaffected by the force of the waves at all sites: damage to these colonies included occasional broken branches (Fig. 2C), presumably as a result of impacts with mobile debris, but very few colonies were dislodged. In contrast, corals growing in unconsolidated substrata, such as sand or rubble, suffered much greater damage: in these habitats many colonies were overturned (Fig. 2D), buried (Fig. 2F), or transported, often over large distances (Fig. 2G). Despite this damage at depth, where coral assemblages were healthy prior to the tsunami, coral cover remained high, and there was little apparent loss of ecological diversity or function.

This type of damage is very different to that observed following large storms, such as hurricanes. While hurricane damage to reefs is also patchy (Woodley et al., 1981), it is unusual for shallow reefs to escape damage over large scales following hurricanes (Hughes and Connell, 1999). Furthermore, fragile morphologies, such as branching and tabular corals, are generally disproportionately affected when compared to massive colonies following hurricanes. A number of features of tsunamis are relevant for explaining this difference. In wind waves, most energy is contained near the surface, and wave-induced water motion decays exponentially with depth (Yeh et al., 1993). In contrast, in a tsunami, water is in motion throughout the entire water column (Yeh et al., 1993). We hypothesise that the initial run down of the tsunami, along with the first wave of the tsunami train, excavated unconsolidated substrata from around the bases of unattached colonies, making them susceptible to displacement when inundated by the subsequent waves. The differential damage to unattached massive colonies at depth appears to be a unique feature of tsunamis disturbance and explains the dominance of massive colonies in tsunami deposits on land (Baird et al., 2005).

An interesting feature of our analysis was that transects with high proportions of up-turned coral did not necessarily have high proportions of broken live coral or recently dead coral. This suggests that the type of damage observed at a site is strongly influenced by what coral species are present. For example, the higher proportion of broken corals on reef crests on Pulau Aceh and mainland reefs compared with Pulau Weh was probably the result of high cover of *Heliopora* (unpublished data), which has a brittle skeleton prone to breakage from mobile debris. *Acropora* colonies, in contrast, did not appear prone to breakage, and were very rarely up-turned, consequently, sites where these species were abundant, such as in the shallow on Pulau Weh had few broken corals. Similarly, large thickets of *Acropora muricata* albeit recently killed (Fig. 2B), remained intact, despite an estimated flow height at the coast of over 15 m (Borrero, 2005) at this site. It is, therefore, surprising that damage to *Acropora* colonies was so prominent in the Seychelles, more than 3000 km from the epicenter of the earthquake, where the maximum wave height was 1.24 m (Hagan et al., 2007).

Ongoing effects of tsunami in April 2005 included an increase in turbidity at many sites where some *Acropora* and faviids were bleached (Fig 2 H), probably as a consequence of prolonged periods of low light (Fabricius, 2005), because there is no indication of recent elevated sea surface temperatures in the area (NOAA, 2005).

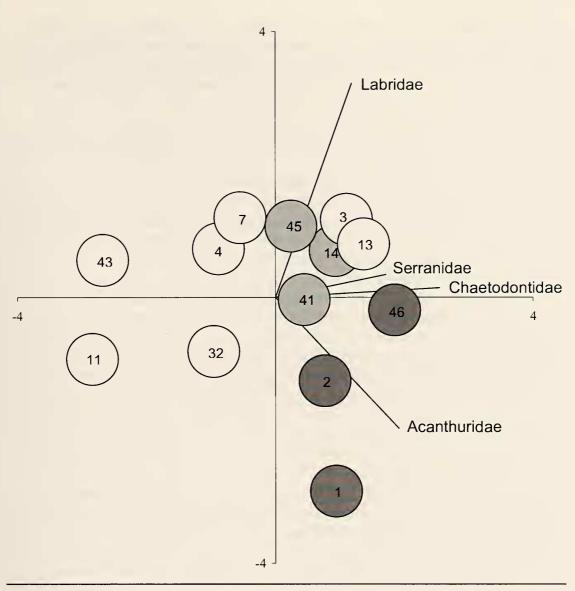


Figure 7. Canonical Discriminant Analysis of coral reef fish assemblages on Acehnese reefs in April 2005. Canonical variates 1 and 2 account for 38.5 % and 26 % of the variation in community structure among all sites and emphasize differences among management regimes (Kawasan Wista = dark grey, Panglima Laut = light grey, and open access = white). Numbers on each centroid correspond with site numbers shown on Figure 1. Circles plotted represent 95% confidence limits around the centroids for each site. Vectors are structural coefficients of response variables, indicating the relative abundance of different families of fishes at each site.

Reef condition varied widely within the region and was strongly influenced by controls on human activity (i.e. management zone). Reef condition was particularly poor in Pulau Aceh (Fig. 4), here long dead colonies and rubble beds were covered with a thick growth of filamentous algae: scenes typical of reefs affected by bombing and cyanide fishing (Pet-Soede et al., 1999). However, even here, where the tsunami was highly destructive on land, there was little evidence of recent coral mortality (Fig. 3C). The most likely cause of low cover at open access sites is destructive fishing practices, such as bombing and cyanide fishing, both of which were prevalent throughout Indonesia in the recent past (Hopley and Suharsono, 2002) and many locals suggested that sediment runoff from inappropriately cleared land may have smothered some reefs (e.g., Lhok Weng – site 11 and Leun Ballee – site 40). On Pulau Aceh, these practices have caused a phase shift (e.g. Hughes, 1994) from corals to algae which the tsunami may have exacerbated with an influx of nutrients and the prospects for recovery of these reefs in the short term are not good.

Given the intensity of the Sumatra-Andaman tsunami, it is again surprising that there was no clear evidence of disturbance to the reef fish assemblages. Tsunamis have the potential to affect fishes by displacing individuals or washing them ashore, as has been observed during severe tropical storms (e.g., Walsh, 1983). Local villagers reported that many small fishes had been washed ashore at Palau Weh immediately after the Sumatra-Andaman tsunami (Allen, 2005). However, it is the disturbance to benthic reef habitats, such as high coral mortality and major alterations in the physical and biological structure of benthic reef habitats, which are most likely to have the greatest impact on coral reef fishes (Wilson et al., 2006). Declines in the abundance of fishes following extensive depletion of hard coral are common (e.g., Sano et al., 1987; Jones and Syms, 1998; Booth and Berretta, 2002; Munday, 2004; Pratchett et al., 2006), though there can be a significant time lag between the loss of habitat and a reduction in fish numbers. For example, Pratchett et al. (2006) detected no change in the abundance of obligate corallivorous cheatodontids, despite a 90% decline in coral cover following coral bleaching, 4 months after the event, which suggests that cheatodontids may take longer than this to starve or relocate. Consequently, the low abundance of cheatodontids at open access sites may indicate that the low coral cover at these sites predated the tsunami. Given that we detected no major change in benthic habitats from the tsunami, as described above, it is, therefore, also highly unlikely that reef fishes were adversely affected by the tsunami. While significant spatial variation in the overall abundance and species richness of coral reef fishes among sites was apparent, this was not attributable to differential affects of the tsunami. For example, the overall abundance of fishes was much higher at Teupin Pineung (site 43), where damage to corals was most pronounced, compared to Anoi Hitam 1 (site 41), where there was very little damage to corals. However, without data from before the event, such conclusions must be treated cautiously.

The relative abundance of some coral reef fishes, especially the Acanthuridae, Serranidae, Labridae and Chaetodontidae, was higher within the Kawasan Wisata (which is closed to all but line fishing) when compared to open access and Pang Lima Laut sites suggesting management has been effective at protecting some species, in particular, those often caught with nets (Russ, 2002). However, total abundance of reef fish did not vary between management zones, and heavily targeted fishes, such as lethrinids, were in low abundance at all sites. Clearly, management of the Kawasan Wisata could be improved. and there was occasional evidence of breaches of regulations, such as discarded nets. However, comparisons among management zones are confounded by differences in the aspect and benthic habitats of regulated areas versus open access areas. The two existing regulated areas, the Kawasan Wisata and Panglima Laut, are both located on the northeast side of Palau Weh. In addition, there is little true reef development on Pulau Weh: in the shallows, corals grow attached to large rocks; at depth Porites bombies which can grow in sand are dominant (unpublished data). In contrast, reefs on Palau Aceh and the mainland are true fringing reefs with potentially greater habitat diversity. This may explain why species richness of fishes within the Kawasan Wisata and Panglima Laut was often lower compared to open access areas. Responses of fishes to protection from fishing are influenced by many complex factors, including the size of reef, the structure of reef fish populations, the proximity of other reefs and the level of compliance with protection regulations (Babcock et al., 1999; McClanahan and Mangi, 2000; Jennings, 2001; Shears and Babcock, 2003; Cinner et al. 2005). Nonetheless, MPAs are gaining increasing acceptance among scientists as one of the few effective ways of managing fisheries of coral reef species (Russ, 2002), and may be critical in making reefs more resilient to acute natural and anthropogenic disturbances (Bellwood et al., 2004).

CONCLUSIONS

Few natural events can compare in scale and intensity to the Sumatra-Andaman tsunami, yet direct damage on reefs was surprisingly limited, and trivial when compared to the clear loss of coral cover where human access has been uncontrolled. The extent of the damage on land, and the tragic human cost should not distract attention away from the perennial problems of marine resource management in Indonesia: improving water quality, reducing fishing pressure and sensible coastal development (Bellwood et al., 2004). Neither the conservation priorities nor the risks to reefs have been changed by the tsunami and it is vitally important that resources are not directed to short term, small scale rehabilitation programs which will not reverse long term declines in reef condition (Hughes et al., 2005). The political good will and the financial resources the tsunami has generated should rather be used to build sustainable economies and just societies that will provide long term security for the people of Aceh and beyond.

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